Selbyana 17: 27–35

CANOPY MAMMAL TRAPPING ON BARRO COLORADO ISLAND, PANAMA: A SIX MONTH SURVEY

DEEDRA MCCLEARN,[1] HEATHER ROMAN, AND SHANNON HORAN

Section of Ecology & Systematics, Division of Biological Sciences, Cornell University, Ithaca, New York 14853

WILLIAM ROSE

P.O. Box 297, Kirkwood, California 95646

ABSTRACT. We constructed a mammal trapping grid in the subcanopy and canopy levels of the Allee Creek watershed on Barro Colorado Island, Panama. We report here the results from a continuous six-month trapping study (July–December 1994) using large (81 × 32 × 26 cm) traps baited with whole bananas. Species diversity of trapped animals was extremely low, with 847 of 862 captures being coatis (*Nasua narica*). Most of these captures were multiple captures of a few adult females. Morning and afternoon capture frequencies were not significantly different. The number of captures was highest during a period of fruit abundance, contrary to expected findings. The spatial pattern of captures indicates that, although females may forage together in bands, their sites of capture do not cluster together. The provision of large single food items widely spaced (bananas in traps) is unlike the normal spacing of food items and seems to alter band dynamics temporarily. The characteristics of the trees with the most coati captures strongly suggests that the presence of lianas stretching between the ground and the tree crown provides access to the canopy.

INTRODUCTION

In many neotropical forests at least half the nonflying mammals spend a portion of their lives in trees, considered both by numbers of species (Janson & Emmons 1990, Fleming 1973) and by total mammalian biomass (Eisenberg 1980, Eisenberg & Thorington 1973, Terborgh 1986). Despite the prominence of this arboreal component of the mammal fauna, many of these species, particularly the small, nocturnal ones, remain poorly known (Malcolm 1995). In recent years, the results of several canopy mammal trapping studies have provided information regarding the vertical stratification of neotropical mammals (Charles-Dominique *et al.* 1981, Malcolm 1990, 1991, McClearn 1992) and the relations between small mammal abundance and diversity on the one hand and vertical and horizontal habitat diversity on the other (Malcolm 1995).

The study reported here is a canopy mammal trapping project conducted on Barro Colorado Island (BCI) in Panama from 1 July to 25 December 1994. We undertook to assess the following: (a) the feasibility of modifying Malcolm's (1990) canopy trapping platform system with the pulley method of trap raising and lowering for large (raccoon-sized) traps, (b) the temporal pattern of trap success and diversity of mammal species captured using continuous trapping over a six-month wet season period, (c) the spatial pattern of mammal captures over the range of a four ha trapping area. Finally, we hoped to provide some insight into the relations between the movement patterns of the animals we captured and the structure of the forest environment in which they live.

MATERIALS AND METHODS

In January of 1993 we established a 5 × 5 trapping grid with traps spaced at 40 meter intervals. Most of the grid was contained within the area encompassed by Barbour Lathrop, Fairchild, and Fausto trails (FIGURE 1) north of the laboratory clearing on BCI. The four ha area covered by the trapping grid is decidedly nonuniform. The southern, western, and northern borders of the grid run close to the trails; the southern border parallels the main branch of Allee Creek, the western border rises in elevation from south to north, and the center of the grid is cut by several steep ravines running NNW to SSE.

For each survey point, a nearby tree was chosen for placement of a wooden trapping frame. The main criteria for tree choices were (1) a straight section of trunk to attach the trapping frame and (2) an understory free of vegetation so traps could be raised and lowered with relative

[1] Author to whom correspondence should be addressed.

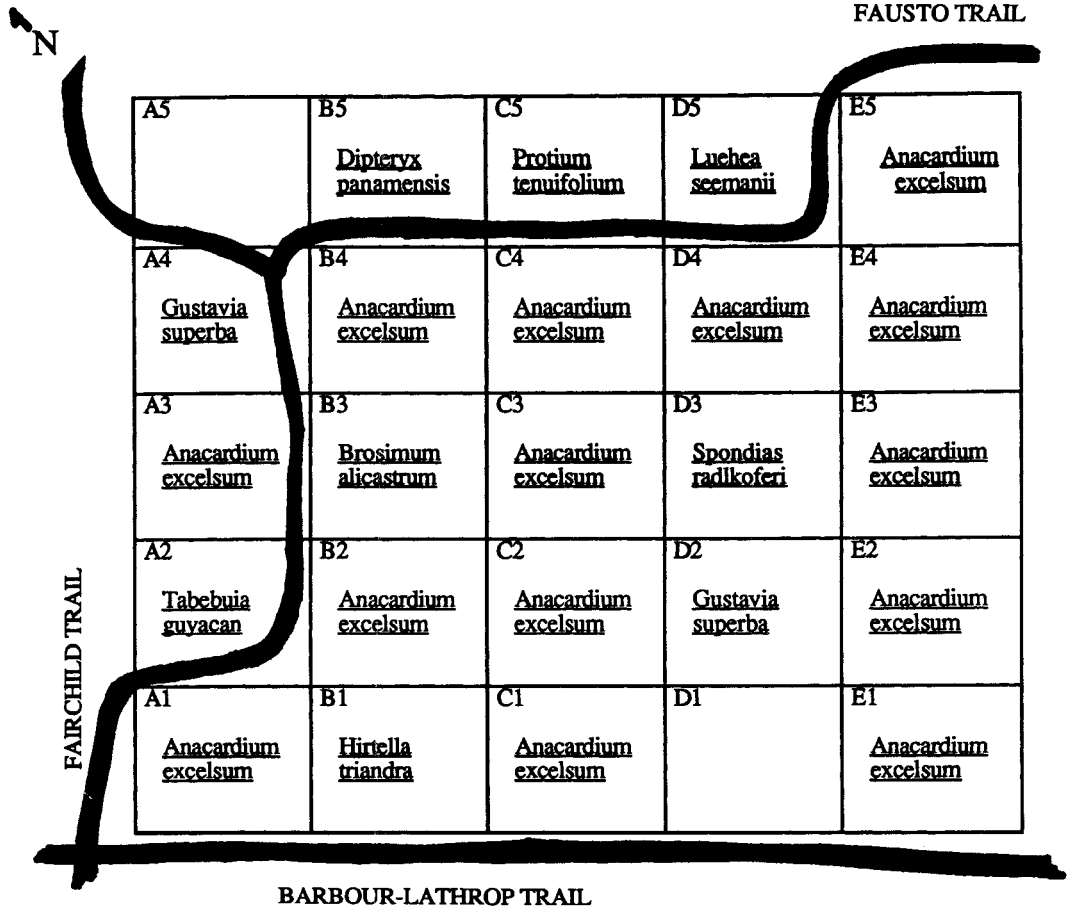

FIGURE 1. Layout of study grid showing trails and the identity of the trees to which trapping platforms were attached. The line running from A1 to A5 is oriented along a 20 degree heading (NNE). The highest point on the grid is a ridge between B5 and C5 that separates the Allee Creek watershed from adjacent systems. The lowest point on the grid is at E1, near where Allee Creek leaves the grid area. This plot is in an area of forest that was disturbed earlier in the century (Leigh & Wright 1990) but is now approaching the undisturbed forest in canopy height and species composition.

ease. Sixteen of the 25 trees chosen were wild cashews (*Anacardium excelsum*); the other nine trees were other canopy and subcanopy species (FIGURE 1).

The trapping frames are a modified version of the design used by Malcolm (1990, 1991, 1995) for his canopy mammal studies in Brazil. Our frames were larger than Malcolm's, to accommodate raccoon-sized (81 × 32 × 26 cm) live traps. We used second growth cedro espino wood (*Bombacopsis quinata*); this wood is moderately hard and is said to have a natural resistance to insect infestation because of its acidic sap. Trapping frames were lifted into the trees with the Yosemite haul system (Setnicka 1980) and fastened with steel cables. Wooden blocks were positioned between tree and cable so that no metal touched the surface of the tree. Cables were tightened with turnbuckles. Traps were raised and lowered from the ground by a length of parachute cord that was tied to the trap, ran through two pulleys attached to the trapping platform, and was affixed at its other end to a small tree trunk near the ground.

As of December 1994 the trapping frames had been in place for approximately 24 mo. Two frames were knocked apart by treefalls between their installation and the beginning of this trapping project. Most remaining frames remained in good shape throughout the study period although three or four sustained termite damage. Nylon webbing (Climb High 1 in tubular nylon webbing) and carabiners left in the trees were intact and functioning throughout the study pe-

riod with one exception. The nylon webbing at E2 was changed every 3 mo because *Azteca* ants in the tree chewed through the nylon repeatedly. The nylon parachute cord (Adventure 16 400-lb-test utility cord) used to haul traps up and down daily was replaced once during the study. This is apparently the element most affected by the trapping conditions; the cord is exposed to the weather and also sustains long periods of time held under tension supporting the weight of the trap. Traps at the A5 and D1 sites were not operating during the trapping period reported here.

For this study Tomahawk live traps were baited with whole bananas and hauled into place during the first three days of July 1994. Traps were checked twice per day (0800–1000 and 1500–1700 hrs) until 25 December. Kinkajous were marked with hair dye, sexed, weighed, and released. Most coatis we caught were already marked with eartags from a previous study (see Gompper & Krinsley 1992). When traps remained open without capturing an animal, bananas were replaced every five days. We also rebaited traps in which an animal had been caught and traps from which bait had been stolen or eaten by insects.

Independent samples *t*-tests for comparing morning and afternoon trap events and trap successes were performed on data grouped by month; variances were not pooled (Wilkinson *et al.* 1992).

Results

Overall trap success. The most striking results from this six month canopy mammal trapping study are the high trap success for coatis (*Nasua narica*) and the exceedingly low trap success for other mammals. There were 847 coati captures, 14 kinkajou (*Potos flavus*) captures (two individuals), and one common opossum (*Didelphis marsupialis*) capture. Overall trap success was 12.7% and trap success for coatis (excluding from the calculations trapping intervals during which other animals were captured) was 12.5%.

There were pronounced age and sex class differences in capture likelihood of coatis. Adult male coatis were not commonly drawn to our traps (17 captures of two marked males), although these two and an additional marked male were regularly observed in the Allee Creek watershed area. We never caught young juveniles (about six mo of age or younger) but we did trap older juveniles of both sexes. On several occasions, two females were caught in the same trap simultaneously.

All animals captured were 1.5–4.5 kg omnivores or frugivores. We never caught white-faced monkeys (*Cebus capucinus*) or tayras (*Eira barbara*) although both species were observed in our trapping area and overlapped in body mass and dietary preferences with the species we did catch. The kinkajou captures were spread over the first five months of the study, with the highest frequency (six captures of one individual) recorded for September.

Temporal patterns of coati captures. Several phenomena are of interest with regard to the temporal patterns of coati captures. The total number of trap "events" (time periods for which a trap was open and could potentially have caught a coati) was 3,340 for the morning trap checks and 3,411 for the afternoon checks; these values are not significantly different ($P = 0.69$). There was no overall significant difference between the number of morning (448) and afternoon (399) coati captures ($P = 0.37$). The number of daylight hours leading up to morning and afternoon checks was also approximately the same, but we do not know whether the majority of coatis found in traps during the morning check had been trapped in the waning daylight hours of the previous day or in the time just prior to the morning check.

A second temporal pattern of coati captures is seen when the data are grouped by month. Calendar months are arbitrary units for this purpose but nonetheless provide six equal time periods covering most of the wet season of 1994 on BCI (Table 1). Coati captures were relatively low in July (3.6%) and August (5.5%), peaked in September (17.8%) and October (21.2%), and subsided somewhat in November (12.0%) and December (12.6%). The increase in trap success during September and October represents primarily an increased frequency of capture of several marked individuals rather than the capture of new animals.

Spatial pattern of coati captures. The analysis of the spatial pattern of coati captures requires consideration of the topography of the plot as well as the behavior of the coatis as individuals and as social groups. The area covered by the grid encompasses trails, ravines, and creek beds but coatis obviously travelled throughout the entire area. The number of coati captures plotted for individual traps yields a normal distribution. Only one trap (B4) on the grid never had a coati capture over the six month period of trapping. All other traps had one or more captures, although some traps seemed to be strongly favored by the coatis over others (see below). Interestingly, one of the kinkajou captures was in the single trap for which there were no coati captures.

A quantitative assessment of the spatial pattern of coati captures is difficult because a few adult females in a single band were responsible for a large percentage of the captures over the wet season. Not only were there multiple measures of the same individual, but the location in

TABLE 1. *Coati trap success by month.* For each of the months of the study the number of coati captures divided by the total number of trapping "events" for that month yields the trap success. A trapping event is the period of time between trap checks when a trap was open and could potentially have recorded a capture. The occasional trap events that produced a kinkajou capture were eliminated from the calculations for coati trap success.

July	32/882	0.036
Aug	72/1,302	0.055
Sept	223/1,256	0.178
Oct	270/1,276	0.212
Nov	137/1,141	0.120
Dec	113/894	0.126
Total	847/6,751	0.125

which an individual was trapped was not independent of the location in which that individual was subsequently trapped.

We charted the spatial arrangement of captures over two separate 14 day periods (15–28 September and 15–28 October) for which four individual adult female coatis were caught, almost without exception, at least one during every 24 hr period (FIGURE 2). Two principal observations can be made from these maps. First, the patterns of captures are distinct for each female for a given time period. For example, coati RGGB was trapped most frequently in the western half of the grid whereas coati XXRB was captured more frequently in the eastern half during the same two-week period in September. Second, the capture pattern for an animal during the first time period does not necessarily correspond to the capture pattern seen the following month. For example, female YR was trapped throughout the central ravine and along the southern border of the grid during the September two-week period whereas her captures in October were confined to a small number of traps in the south central area, with two forays in the northeastern edge of the grid. TABLE 2 provides a key to the maps in FIGURE 1 and reveals two other patterns of captures of these coatis. At any given trap check, these four females are usually not found in adjacent traps. For example, at the morning check on 28 Sept, these animals were in traps A4, C2, C5, and E1. At the morning check on 24 Oct they were in A3, B2, D5, and E2. Both sets of locations are distributed across the watershed area. Also, a particular coati may be caught frequently in a particular trap during one time interval and then move to another area. For example, RGGB was in C2 five times between 15 and 18 Oct and then not again for the next ten days.

There were several time periods during which an individual coati would be found in a trap at several successive trap intervals, sometimes repeatedly in the same trap. Body mass measurements for these animals generally did not fluctuate more than 0.5 kg and there was no indication that animals were losing weight either over these short time periods or over the length of the entire study. Because two bananas per day would not provide sufficient energy to sustain body mass, the coati females were presumably foraging elsewhere between captures.

Characteristics of trees with highest coati trap success. The trees with traps that had the most coati captures were spread across the grid, they represent the full complement of tree species diversity, and they span the full range of trap height and tree dbh (TABLE 3). It appears, therefore, that grid topography, tree species, tree size, and trap height do not determine the likelihood of a coati capture.

One factor that may affect coati trap success is the access to the tree crown by lianas. Of the 11 traps with less than 10% trap success, eight had a liana access score of 0, whereas only one of the 12 traps with greater than 10% trap success had no lianas spanning the ground–crown gap. Among dozens of observations of coatis climbing up to the traps and hundreds of filmed sequences of coatis being released from traps that had been lowered to the ground, we always observed coatis using vines and lianas and small diameter understory trees to get into the crowns of trees >50 cm dbh. C2, the large diameter tree with the highest trap success and a liana score of 0 (meaning no free-hanging lianas), had a series of helically wound vines on the tree trunk that coatis used as a spiral access path to the C2 trap.

DISCUSSION

Canopy trapping techniques. Canopy access techniques are a source of interest and concern for biologists working in the treetops (Moffett & Lowman 1995). We found the logistics of running a canopy trapping grid with large traps were not unreasonable once the grid was established. However, it took approximately five weeks to survey the grid, shoot lines into the trees, build the platforms, and fasten the platforms into place. The major problems in running the grid were parachute cord getting stuck in the pulleys, rebaited traps closing as they were hauled into position, and tree falls knocking our platforms apart. We replaced several pulleys with metal rings over the course of the study. We also used two-person teams to run trap checks so one person could maneuver the trap with a guy line while the other person hauled the trap into position. We had no solution for the tree fall problem.

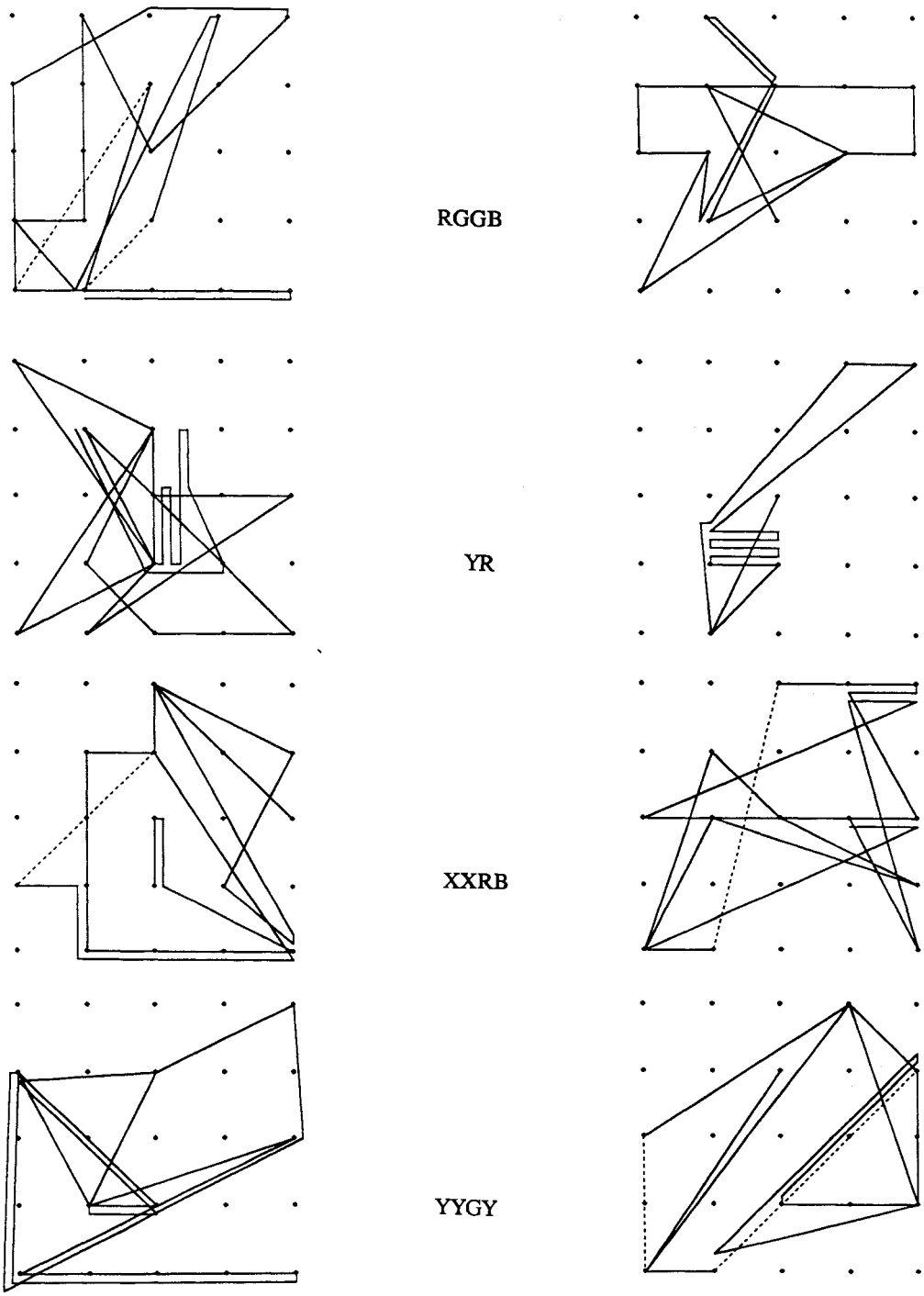

FIGURE 2. Maps of capture locations of four individual female coatis over two separate two-week periods. The dot matrix represents the trapping grid and is oriented as shown in FIGURE 1 (trap A1 in the bottom left corner, trap E5 in the upper right corner). The four maps on the left side of the figure are the capture locations for four coati females during a two-week period in September (15th–28th) and the four maps on the right side are the capture locations for these same coatis during a two-week period in October (15th–28th). Individual coati identities are indicated by the sequence of letters between September and October maps (RGGB, YR, XXRB, YYGY). The key to the trap locations, dates and coati identities is provided in TABLE 2. The spatial pattern of captures appears to be independent for different coatis on the same day and for the same coati during different time periods.

TABLE 2. *Coati captures over two-week intervals in two successive months.* Coati identity is shown in the top line (RGGB, YR, XXRB, YYGY) and trap sites at successive trap checks are shown in the body of the table. These trap locations provide a key to the maps in Figure 2. AM and PM refer to morning and afternoon checks. * Coati YR was released from B2 at the afternoon trap check on 22 September and was found caught in C1 by the time we reached that trap some minutes later.

	RGGB		YR		XXRB		YYGY	
Date	AM	PM	AM	PM	AM	PM	AM	PM
9.15	—	A1	C3	E3	—	C2	B2	—
9.16	—	—	—	—	C3	—	C2	E3
9.17	—	C4	B1	C2	C2	—	E3	B2
9.18	—	—	C3	C4	E1	B1	A4	C2
9.19	B1	—	A5	C2	B4	—	A1	—
9.20	—	—	—	C2	—	C4	—	—
9.21	C2	D5	A1	C4	—	—	E1	A1
9.22	—	B1	C4	B2/C1*	—	A2	A4	—
9.23	—	A2	E1	B4	—	B2	A1	—
9.24	B2	B5	C2	C3	B1	E5	A1	E3
9.25	C3	E5	C2	C3	C4	C5	E5	C4
9.26	D5	C5	C4	C3	E4	D2	B2	C2
9.27	A4	A1	D2	—	E1	—	—	—
9.28	E1	B1	C2	B4	C5	E3	A4	C4
10.15	C2	—	B1	C2	D3	B3	E4	D5
10.16	—	C2	B2	B2	A1	B1	—	—
10.17	C2	C2	B2	B2	—	—	A1	B1
10.18	C2	B4	B2	B2	—	—	—	—
10.19	B4	D3	C2	B2	—	—	—	E4
10.20	B2	B2	C2	C2	C5	—	E2	—
10.21	C4	B5	B2	—	E5	D5	C2	C2
10.22	C4	C4	—	E5	—	E3	E4	B1
10.23	B2	B3	D5	D5	D3	E1	—	—
10.24	A3	A4	B2	B2	D5	E5	E2	D5
10.25	B4	—	—	—	A3	B3	—	A3
10.26	E4	E3	B1	—	E2	C3	—	—
10.27	D3	D3	C3	—	B4	A1	A1	—
10.28	A1	B3	—	—	E3	D3	—	C4

Species diversity. In six months of trapping we had only three species represented, with the vast majority of captures from a single species, the white-nosed coati. This is lower diversity than is seen in studies using smaller traps (Malcolm 1995, McClearn *et al.* 1994), presumably because the small arboreal rodents and opossums do not set off the closing mechanism of the large traps. We continue to record higher species diversity using small traps and automatic cameras both on BCI and on Gigante Peninsula (McClearn unpubl. data). Other factors that may have contributed to this low diversity include choice of bait, a residual smell of coatis in the traps, or difficulty on the part of some species in reaching the trapping platform. Coati densities on BCI have been considered by some to be unnaturally high (Terborgh & Winter 1980), although others have suggested that coati densities are within natural bounds (Glanz 1990).

Most of our coati captures were of adult females. Adult males were present on our site but represent only 17 of 847 coati captures. Males may be less inclined either to enter traps or to climb trees than females, although this first possibility seems unlikely as we caught adult males on the ground in the Allee Creek watershed before and after our canopy trapping study. Smythe (1970) suggested that the sexual size dimorphism in coatis may represent a partitioning of feeding niches between the sexes but as yet there are no experimental data on sex differences in climbing behaviors of coatis.

The timing of the reproductive season probably had little effect on the age and sex class composition of our captured coatis since our trapping period occurred well after young are born in April and before the mating season in January (Kaufmann 1962, Russell 1982, Gompper 1995). We caught neither young of the 1994 breeding season nor lactating females.

Temporal pattern of captures. All the kinkajou and opossum captures were recorded at the morning trap check and probably represent captures that occurred during the night. Coati captures were not significantly different in number

TABLE 3. *Characteristics of trees with highest coati trap success.* Liana access is a score for the number of lianas stretching from the ground beneath the tree into the crown with 0 meaning no lianas, 1 is 1–3 lianas, 2 is 4–6 lianas and 3 is more than 6 lianas.

Tree	Trap success	Captures/events	Genus	Trap height (m)	DBH (m)	Liana access
C2	34.6%	(109/315)	*Anacardium*	15	90	0
B2	27.2%	(86/316)	*Anacardium*	20	70	1
A4	26.2%	(85/325)	*Gustavia*	9	20	1
D5	21.1%	(64/304)	*Luehea*	12	50	3
B3	19.8%	(51/258)	*Brosimum*	10	40	1
D3	17.2%	(40/233)	*Spondias*	10	55	1
A1	16.7%	(54/323)	*Anacardium*	14	90	1
B1	13.8%	(47/340)	*Hirtella*	8	40	1
C3	12.6%	(33/261)	*Anacardium*	14	65	1
E5	12.3%	(36/292)	*Anacardium*	17	70	2
C4	11.3%	(55/486)	*Anacardium*	15	65	2
E1	11.3%	(38/335)	*Anacardium*	13	55	1

for the morning and afternoon trap checks. Coatis on BCI generally forage throughout the daylight hours, with a rest period at midday (Kaufmann 1962, Gompper 1995), so a coati recorded at the afternoon check entered the trap somewhere roughly between 1000 and 1500 hrs (midday) whereas a coati recorded at the morning check probably entered the trap either between 1500 hrs and sunset (1830 hrs) or between sunrise and the morning trap check (0600 to 0900).

The monthly pattern of coati captures shows lowest trap success in July and August and highest trap success in September and October. The kinkajou captures also peaked in September, although the sample size is small and represents only one individual. On BCI and surrounding areas, mammal trap success is usually highest when fruit abundance is lowest (Glanz 1982, McClearn *et al.* 1994) but fruit availability is not inversely associated with trap success in this study. Major periods of fruit shortage generally come in dry season (December through March) and the middle of wet season (July and August) (Foster 1982). A peak in fruit abundance occurs in September and October, coinciding with our months of highest trap success. A more likely explanation for the pattern of trap success in this study concerns differential trappability of species and individuals. Perhaps kinkajous, opossums, and other 2–4 kg arboreal animals are less likely to be trapped than coatis, and, once trapped, less likely to be retrapped. In contrast, certain individual coatis apparently become trap-happy and their likelihood of capture increases over time.

Spatial pattern of captures. Coati females and young of both sexes sleep and forage together as a social unit, whereas adult males are usually solitary (Gompper 1995). The coati females caught most frequently in our study were members of the same band and were seen foraging or travelling together before, during, and after our trapping period. There is evidence that coati social structure is influenced by food availability (Gompper & Krinsley 1992, Kaufmann *et al.* 1976). The movement patterns and band dynamics of the coatis were also influenced by our manipulations of food availability and the retention of band members in traps while the rest of the band moved away.

The pattern of captures for these band members suggests, however, that the trap a female entered was not determined by its proximity to a trap a fellow band member entered during the same trap interval. In other words, band members were not spatially clustered at a particular trap check. Nor did individual females stake out a few traps and enter the same subset of traps throughout the study. Rather, an individual seemed to move between adjacent traps on subsequent occasions for a few days and then move to a different part of the grid.

The female coatis caught most frequently in our study behaved as if they knew the location of the traps or at least could pinpoint the scent of bananas. On several occasions we released an animal and watched it head directly to an adjacent trap location, where we would find it captured at the next trap check. Occasionally a coati would pass by as we were rebaiting a trap, climb to the platform as we raised the trap, and enter the trap as soon as it was tied off. Clearly the behavior of these animals was being influenced by the trapping conditions.

Characteristics of trees with the most coati captures. Many factors could influence which traps had the greatest number of coati captures, including trap height, ease of access to the trapping platform, and species of tree in which the trap

was located. Our traps ranged in height from 6 to 25 m above ground and the trees varied in diameter from 20 to 120 cm. If we consider the overall differences between the most "popular" traps (12 traps with trap success > 10%) and compare them to the others (11 traps with trap success < 10%), it does not appear that trap height, tree species, or tree diameter differ between the two groups. The main distinction between the two groups of trees is the presence of lianas stretching from the ground to the tree crown. Among the trees with the most coati captures, all but one had lianas running vertically into the crown. The single tree without free-hanging lianas had a mass of small diameter vines wound around the tree trunk. Eight of the 11 trees with fewest coati captures had no lianas spanning the distance from ground to crown. Our behavioral observations of the coatis confirm the importance of lianas as access routes to the forest canopy. We have never observed a coati scale a large diameter (>50 cm) smooth tree trunk but we have recorded hundreds of ascents of lianas, vines, small (10–30 cm) tree trunks, and large trunks wrapped with twining vines, as well as short horizontal traverses from one crown to an adjacent one (McClearn 1992). A 50 cm cut-off diameter is also what one would predict for an animal the size of a coati using a static friction grip on a fairly smooth surface (Cartmill 1985).

Our evaluation of the role of lianas in coati movements echoes the assessments in two recent papers on canopy mammals of neotropical forests (Emmons 1995, Malcolm 1995). Both these authors stress the importance of connectivity in the canopy and the association between canopy lianas and faunal richness. There are potentially interesting implications for conservation if liana densities and spatial arrangements are important components of forest structure for nonflying mammals. Lianas have only recently been recognized as a dominant part of the forest vegetation (Gentry 1985, Gentry & Dodson 1987, Putz 1984), but lianas are usually considered a nuisance or a serious threat to the canopy trees (Clark & Clark 1990, Putz 1980, 1988). If a forester's goal is to preserve species biodiversity (including mammals) and if it is in a tree's best interests to permit access by mammals (e.g. for pollination or seed dispersal), then a moderate density of lianas may indeed be the sine qua non of a healthy neotropical forest.

Acknowledgements

We would like to thank many people for their assistance. Dr. Rob Roy Ramey II designed the giant slingshot used to propel lines into the canopy. Dr. Kevin J. McGowan and Dr. William E. Glanz helped survey the grid during initial setup in 1993. Dr. Milo E. Richmond and Dr. Nicholas Smythe lent us the large live traps. Elena Cedeño, Claudio Carrasco, Tonya Rawlings, Chris Fitzgerald, and Holly Bardon helped run the trapping grid during the six-month period reported here. Dr. Greg Gilbert climbed many trees to replace pulleys with metal rings when the parachute cord got stuck. This project was supported by the President's Council on Cornell Women, the Polartec Corporation, and como siempre, Nancy and Gerald McClearn.

Literature cited

Cartmill M. 1985. Climbing. Pp. 73–88 *in* M. Hildebrand *et al.*, eds., Functional Vertebrate Morphology. Belknap Press of Harvard University, Cambridge, Massachusetts.

Charles-Dominique P. M., M. Atramentowicz, M. Charles-Dominique, H. Gerard, A. Hladik, C. M. Hladik, and M. F. Prévost. 1981. Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: interrelations plantes-animaux. Revue Ecol. (Terre et Vie) 35: 341–435.

Clark D. B. and D. A. Clark. 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. J. Trop. Ecol. 6: 321–331.

Eisenberg J. G. 1980. The density and biomass of tropical mammals. Pp. 35–55 *in* M. E. Soule and B. A. Wilcox, eds., Conservation Biology: An Evolutionary Perspective. Sinauer Press, Sunderland, Massachusetts.

——— and R. W. Thorington, Jr. 1973. A preliminary analysis of a neotropical mammal fauna. Biotropica 5: 150–163.

Emmons L. H. 1995. Mammals of rain forest canopies. Pp. 199–223 *in* M. D. Lowman and N. M. Nadkami, eds., Forest Canopies. Academic Press, New York, New York.

Fleming T. H. 1973. Numbers of mammal species in North and Central American forest communities. Ecology 54: 555–563.

Foster R. B. 1982. The seasonal rhythm of fruit fall on Barro Colorado Island. Pp. 151–172 *in* E. G. Leigh, Jr., A. S. Rand and D. M. Windsor, eds., The Ecology of a Tropical Forest: Seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, District of Columbia.

Gentry A. H. 1985. An ecotaxonomic survey of Panamanian lianas. Pp. 29–42 *in* W. G. D'Arcy and M. D. Correa A., eds., The Botany and Natural History of Panama. Missouri Botanical Gardens, Saint Louis, Missouri.

——— and C. Dodson. 1987. Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19: 149–156.

Glanz W. E. 1990. Neotropical mammal densities: how unusual is the community on Barro Colorado Island, Panama? Pp. 287–313 *in* A. H. Gentry, ed. Four Neotropical Forests. Yale University Press, New Haven, Connecticut.

GOMPPER M. E. 1995. *Nasua narica.* Mammalian species 487: 1–10.

——— AND J. S. KRINSLEY. 1992. Variation in social behavior of adult male coatis (*Nasua narica*) in Panama. Biotropica 2: 216–219.

JANSON C. H. AND L. H. EMMONS. 1990. Ecological structure of the nonflying mammal community at Cocha Cashu Biological Station, Manu National Park, Peru. Pp. 314–338 *in* A. H. GENTRY, ed., Four Neotropical Forests. Yale University Press, New Haven, Connecticut.

KAUFMANN J. H. 1962. Ecology and the social behavior of the coati, *Nasua narica,* on Barro Colorado Island, Panama. University of California, Publications in Zoology 60: 95–222.

———, D. V. LANNING, AND S. E. POOLE. 1976. Current status and distribution of the coati in the United States. J. Mammal. 57: 621–637.

LEIGH E. G., JR. AND S. J. WRIGHT. 1990. Barro Colorado Island and tropical biology. Pp. 28–47 *in* A. H. GENTRY, ed., Four Neotropical Rainforests. Yale University Press, New Haven, Connecticut.

MALCOLM J. R. 1990. Estimation of mammalian densities in continuous forest north of Manaus. Pp. 339–357 *in* A. H. GENTRY, ed., Four Neotropical Forests. Yale University Press, New Haven, Connecticut.

——— 1991. Comparative abundances of neotropical small mammals by trap height. J. Mammal. 72: 188–192.

——— 1995. Forest structure and the abundance and diversity of neotropical small mammals. Pp. 179–197 *in* M. D. LOWMAN and N. M. NADKARNI, eds., Forest Canopies. Academic Press, New York, New York.

MCCLEARN D. 1992. Locomotion, posture, and feeding behavior of kinkajous, coatis, and raccoons. J. Mammal. 73: 245–261.

———, J. KOHLER, K. J. MCGOWAN, E. CEDEÑO, L. G. CARBONE, AND D. MILLER. 1994. Arboreal and terrestrial mammal trapping on Gigante Peninsula, Barro Colorado Nature Monument, Panama. Biotropica 26: 208–213.

MOFFETT M. W. AND M. D. LOWMAN. 1995. Canopy access techniques. Pp. 3–26 *in* M.D. LOWMAN and N. M. NADKARNI, eds., Forest Canopies. Academic Press, New York, New York.

PUTZ F. E. 1980. Lianas vs. trees. Biotropica 12: 224–225.

——— 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65: 1713–1724.

——— 1988. Woody vines and tropical forests. Fairchild Trop. Gard. Bull. October: 5–13.

RUSSELL J. K. 1982. Timing of reproduction by coatis (*Nasua narica*) in relation to fluctuations in food resources. Pp. 413–431 *in* E. G. LEIGH, JR., A. S. RAND, AND D. M. WINDSOR, eds., The Ecology of a Tropical Forest: Seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, District of Columbia.

SETNICKA T. J. 1980. Wilderness Search and Rescue. Appalachian Mountain Club, Boston, Massachusetts.

SMYTHE N. 1970. The adaptive value of the social organization of the coati (*Nasua narica*). J. Mammal. 51: 818–820.

TERBORGH J. 1986. Community aspects of frugivory in tropical forests. Pp. 371–384 *in* A. ESTRADA AND T. H. FLEMING, eds., Frugivores and Seed Dispersal. Dr. W. Junk Publishing, Dordrecht, The Netherlands.

——— AND B. WINTER. 1980. Some causes of extinction. Pp. 119–133 *in* M. E. SOULÉ AND B. A. WILCOX, eds., Conservation Biology: An ecological-evolutionary perspective. Sinauer Press, Sunderland, Massachusetts.

WILKINSON L., M. HILL, AND E. VANG. 1992. SYSTAT for the McIntosh, Version 5.2. SYSTAT, Inc., Evanston, Illinois.